

REPORT DOCUMENTATION PAGE				Form Approved OMB No. 0704-0188	
Public reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden to Washington Headquarters Service, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington, VA 22202-4302, and to the Office of Management and Budget, Paperwork Reduction Project (0704-0188) Washington, DC 20503.					
PLEASE DO NOT RETURN YOUR FORM TO THE ABOVE ADDRESS.					
1. REPORT DATE (DD-MM-YYYY) 23/11/99		2. REPORT DATE 23 November 1999		3. DATES COVERED (From-To) 1 Dec 99 - 30 Sept 99	
4. TITLE AND SUBTITLE  Advances in the Study of Echolocation in Bats and Dolphins				5a. CONTRACT NUMBER	
				5b. GRANT NUMBER N00014-99-1-1039	
				5c. PROGRAM ELEMENT NUMBER	
6. AUTHOR(S) Jeanette A. Thomas				5d. PROJECT NUMBER 99PR02312-00	
				5e. TASK NUMBER	
				5f. WORK UNIT NUMBER	
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) Western Illinois University Office of Grants & Contracts 320 Sherman Hall Macomb IL 61455				8. PERFORMING ORGANIZATION REPORT NUMBER	
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES) Office of Naval Research ONR 242: Saide B. Marshall Ballston Centre Tower One 800 N Quincy St. Arlington VA 22217-5660				10. SPONSOR/MONITOR'S ACRONYM(S)  ONR	
				11. SPONSORING/MONITORING AGENCY REPORT NUMBER	
12. DISTRIBUTION AVAILABILITY STATEMENT Approved for Public Release; distribution unlimited					
13. SUPPLEMENTARY NOTES					
14. ABSTRACT The grant supported the costs of coordinating and editing a book entitled Echolocation in Bats and Dolphins. The contents stemmed from an ONR Workshop on Biological Sonars held in Portugal during 1998. The book contains sections on: Echolocation Signal Production, Feedback and Control Systems, Auditory Systems in Echolocating Mammals, Performance and Cognition in Echolocating Mammals, Ecological and Evolutionary Aspects of Echolocating Mammals, Echolocation Theory, Analysis Techniques and Applications, and Possible Echolocation in Other Mammals. The book is forthcoming by the University of Chicago Press.					
15. SUBJECT TERMS					
16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT	18. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON
a. REPORT	b. ABSTRACT	c. THIS PAGE			19b. TELEPHONE NUMBER (Include area code)

19991202 129



23 November 1999

Dr. Robert Gisiner  
Scientific Officer  
Biological Sciences & Technology Program  
Office of Naval Research, Code 341  
800 North Quincy Street  
Arlington, VA 22217-5660

Dear Dr. Gisiner;

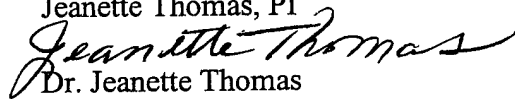
Attached are three copies of the Final Technical Report on the ONR sponsored project entitled "Advances in the Study of Echolocation in Bats and Dolphins", funded under Grant Number N00014-99-1-0139, covering work from 1 December 1998 to 30 September 1999.

In accordance with the ONR contract, I am mailing copies of this final report with specified number of copies as listed below.

Thank you for all your help on this project, call me if you have any questions or need more copies of the final report.

Sincerely yours,

Jeanette Thomas, PI



Dr. Jeanette Thomas  
Western Illinois University Regional Center  
3561 60th St.  
Moline, IL 61265  
Tel: 309-762-9481  
E-mail: Jeanette\_Thomas@ccmail.wiu.edu

Copies Mailed to:

John Chiappe (1)  
Administrative Grants Officer  
Office of Naval Research  
Chicago Regional Office  
Federal Building, Room 208  
536 South Clark St.  
Chicago, IL 60605-1588

Office of Naval Research (1)  
Attn: ONR 00CC1  
Ballston Centre Tower One  
800 North Quincy St.  
Arlington, VA 22217-5660

Director, Naval Research Laboratory (1)  
Attn: Code 5227  
4555 Overlook Drive  
Washington, DC 2037505326

Defense Technical Information Center (2)  
8725 John J. Kingman Road  
STE 0944  
Ft. Belvoir, VA 22060-6218

John Hobbs (1)  
Office Sponsored Projects  
320 Sherman Hall, WTU  
Macomb, IL 61455



## FINAL TECHNICAL REPORT

**Grant Number:** N00014-99-1-0139

**Principal Investigator:** Dr. Jeanette A. Thomas  
Western Illinois University Regional Center  
3561 60th St.  
Moline, IL 61265  
Tel: 309-762-9481  
E-mail: Jeanette\_Thomas@ccmail.wiu.edu

**Grant Title:** Advances in the Study of Echolocation in Bats and Dolphins

**Reporting Period:** 1 December 1998 to 30 September 1999

**Award Period:** 1 December 1998 to 30 September 1999

**Objectives:**

- Develop a proposal and outline of the book
- Secure a publisher
- Review and revise manuscripts in a timely manner
- Submit the book for publication

**Approach:**

A scientific organizing committee planned a conference on biological sonars held 27 May to 2 June 1998 in Carvoeiro, Portugal. The meeting was hosted by a Local Committee and Zoomarine in Albufeira. Five days of meetings had 55 oral and 37 poster presentations by international experts studying animals that echolocation, primarily bats and dolphins. Scientists from the UK, Canada, USA, Germany, Japan, Portugal, Holland, China, Russia, Denmark, Sweden, Israel, Switzerland, and Poland participated. This meeting follows a series of conferences on echolocation in animals held at Frescati in 1966, at Jersey in 1979, and at Helsingor in 1986. Books were published after previous conferences. Participants divided into six working groups and decided on the format and outlined contributions for a book.

Interactions among scientists in the bat and dolphin community during the three previous Biosonar Conferences largely set the direction of research on biological sonars. Examination of the books from these conferences (Busnel, 1967; Busnel and Fish, 1980; Nachtigall and Moore, 1988) demonstrated the continuity of research efforts over time, the impact of new directions of research, and the importance of coordinating research between scientists studying bats and dolphins. Often researchers identified a natural adaptation or ability possessed in an echolocating mammal, perfected over evolutionary time, that had direct application on human-made sonar systems. Because of the importance of sonars in military applications, ONR has been a prominent funding source for echolocation studies on both bats and dolphins. Publishing a book from this conference is the best and quickest way to assemble the latest information from each of the contributors into one single source. The money in this grant was used to cover equipment, commodities, and labor costs associated with publication of such a book.



**Accomplishments (whole project):**

The following prospectus was submitted to the University of Chicago Press and a contract issued to the editors for publication.

**NATURE AND SCOPE OF THE BOOK**

**TITLE:** *Echolocation in Bats and Dolphins*

**EDITORS:** Jeanette Thomas, Laboratory of Sensory Biology, Western Illinois University, Moline, IL 61265; Cynthia Moss, Department of Psychology, University of Maryland, College Park, Maryland 20742; & Marianne Vater, Institut für Zoophysiologie der Universität, Potsdam, Germany

**EDITOR'S PREVIOUS EXPERIENCE:** All editors have extensive editorial experience. Please find the Curriculum Vitae for each editors in Appendix I.

**PUBLISHER:** University of Chicago Press, 5801 Ellis Avenue, Chicago, IL 60636-1496  
Editor of Biological Sciences, Christina Henry, tel: 773-702-0468; fax 773-702-9756 E-mail: cxh@press-mail.uchicago.edu

**ESTIMATED PAGES IN BOOK:** Large size format, of 8.5" X 11", with 900-1000 words per page. Total book length 600 pages, inclusive of indices and glossary.

**COVER ART:** Artwork for the book cover will be provided by the Exhibits Department of the Shedd Aquarium.

**SUMMARY OF BIOSONAR CONFERENCE:**

Nearly 100 scientists from around the world attended a 5-day workshop held in late May 1998 at Carvoeiro Portugal to compare echolocation abilities in bats and dolphins. Oral presentations were given by experts studying echolocation in these two groups of mammals. Posters were presented by graduate and post-doctoral students. The agenda, titles, and authors are provided on a webpage--  
<http://www.wiu.edu/users/mibiol/facstaff/jat/sonar.htm>

At this meeting, participants met in 6 working groups to outline sections for a book. Both bat and dolphin experts were assigned as group leaders. Section leaders are responsible for overseeing that papers for the book are submitted to the editors in a timely fashion.

**GOALS FOR BOOK:**

*Advances in the Study of Echolocation in Bats and Dolphins* presents a unique perspective on animal sonar systems, bringing together introductory chapters on echolocation that are aimed at a general scientific audience and exciting new findings that



are of great importance to experts in the field. The book will include comprehensive overviews of past and current research; it will also emphasize scientific challenges and future directions of study. Where data are available, authors will compare and contrast research findings obtained from bats and dolphins, highlighting the generalized and specialized operations of echolocation in air and under water.

The book will contain six major sections, and each major section will include introductory chapters that outline our the current state of knowledge about bat and dolphin sonar. The authors of the introductory chapters are leaders in the field of echolocation and internationally renowned scholars. The introductory chapters will provide the background and context for understanding more detailed discussions of recent scientific findings that will follow in each section. The Current Research Papers included in each section will present cutting-edge results that will serve as a valuable resource to a wide scientific community.

To our knowledge, no other publication bridges work on bat and dolphin echolocation as we propose to do in this volume. We believe that the book will attract an interdisciplinary audience, drawing attention from students and professionals in the fields of anatomy, physiology, ecology, ethology, hearing science, psychology, physics, engineering and oceanography. The book could serve as a text for college or graduate level courses in animal behavior, bioacoustics and biosonar.

#### **FORMAT OF EACH SECTION:**

One to three introductory chapters, coauthored by experts on the topic, describe the state of knowledge, appropriate methods of study, challenges facing researchers, and promising new directions of study. Introductory chapters address information that is common to both bats and dolphins, present information that is different between the two groups, and emphasize why differences occur.

No color plates will be accepted; however, authors can reference a webpage that gives the figures in color.

Literature Cited should be that of the Journal of Mammalogy.

Each paper will be limited to 1 figure or table per 2 printed pages e.g., a paper that is 10 published page will have no more than 5 tables/figures. Page limit is 15 published pages (or 180 pages of book).

Manuscripts should be submitted on diskette in MSWord or WordPerfect software. We will convert any Mac diskettes to this format. Submit manuscripts on diskette and a hard copy to Jeanette Thomas (address above).

See instructions provided by publisher for format of headings, margins, indentations, tables, and figures.

Authors can either submit hard copies of figures or submit on diskette (following instructions provided by publisher).

Current Research Papers should use these headings:

Abstract, Introduction, Methods and Materials, Results, Discussion, Acknowledgments, Literature Cited.



Introductory Chapters can use any heading format, but consider sections such as: Previous Research, Current Knowledge and Trends, and Future Hot Topics.

Current Research Papers associated with each introductory chapter will illustrate "hot" research topics and methods used to study echolocation abilities in bats and dolphins. Page limit is 7 published pages per paper (or 378 pages of the book).

#### **SCHEDULE FOR BOOK:**

Outline of section due to editors, 1 June 1998

Outline and abstracts of paper due to editors & section leaders, 1 October 1998

Circulate abstracts of papers to all contributors, 7 October 1998

First draft of paper due to editors, 15 January 1999

Paper submitted to 2 external reviewers, 1 February 1999

Comments by external reviewers and editors returned to authors, 15 December 1999

Authors submit final version of paper to editors, 15 January 2000

Editors submit final book to publisher, 15 March 2000

#### **EDITORIAL PROCEDURES:**

Each manuscript will be reviewed by 2 external referees. If these reviewers judge the manuscript not worthy of publication, the paper will be rejected. After external review, the three editors will simultaneously review each manuscript. Thomas will edit each manuscript for proper heading format, margins, literature cited style, letter size and font, identify key words, and create the glossary. Moss will edit the format of figures and tables. Vater will cross check references listed in the text with those cited in the Literature Cited section. When appropriate, editors will suggest ways to cross reference papers in the book. Editors will carefully edit each manuscript to make them accessible to the lay public. To enhance the usefulness as a textbook, keywords will be printed in bold with a glossary of terms at the end of the book.

All comments will be submitted to the author for revision. After final revision by the author(s), Thomas will proof each manuscript. Hardcopy and diskette versions (MSWord) of each manuscript will be submitted to the University of Chicago Press. The editors request an electronic version of final proofs to facilitate preparation of the indices. Moss will prepare the Author Index. Vater will construct the Subject Index.



The current Table of Contents follows with designation of those manuscripts received and submitted to two external reviewers (i.e., D).

## TABLE OF CONTENTS

### **Preface and Acknowledgments**

D This section briefly describes the Biosonar Conference and acknowledges funding sources.

### **Introductory Chapter**

D Au, W. W. L. A Comparison of the Sonar Capabilities of Bats and Dolphins.  
University of Hawaii

### **Section I: Echolocation Signal Production, Feedback, and Control Systems**

D Vocal Control and Acoustically-guided Behavior in Bats by Gerd Schuller from the University of Munich & Cynthia Moss from the University of Maryland.

Like other terrestrial mammals, sounds produced by bats have a laryngeal origin and have been well documented. The authors discuss audio-vocal feedback control and neural circuitry mediating audio-vocal interactions in echolocating bats. No such data are available for dolphins.

#### Current Research Papers on Bats-

- D 1. Behrend & Schuller (University of Munich)-Binaural aspects of Doppler shift compensation in the horseshoe bat, *Rhinolophus rouxi*. Authors discuss how directional cues in echoes of orientation calls influence the Doppler shift compensation systems of bats.
- D 2. Wilson & Moss (University of Maryland)-Sensory-motor behavior in free-flying FM bats during target capture. Authors focus on stereotypic behavioral strategies immediately prior to target capture, including "pulse emission gaps" occurring at consistent intervals before contact, as well as stereotypical wingbeat and flight path patterns which together may provide clues about the information necessary to calculate a motor program for target interception.

Dolphin Signal Production by Ted Cranford from San Diego State University and Mats Amundin from the Kolmarden Zoo.

In this introductory chapter, the authors examine the anatomical and physiological mechanisms for sound production in dolphins. The mechanisms are different from those of bats, due in part to the highly modified nasal and laryngeal tracts and to the requirements for transmission of sound in water. Much of current research concentrates on documenting basic signal characteristics of different odontocete species.

#### Current Research Papers on Dolphins-

1. Ridgway, Carder, Kamolnick, & Root (Space and Naval Warfare Systems Center)-Nasal Pressure and sound production in white whales and bottlenose dolphins during echolocation: timing the decision process. From animals trained to



accept a pressure sensor in the blowhole, the authors measured the perception time and motor time of responses.

- D 2. Nakamura & Akamatsu (Hokkaido University)-Comparison of click characteristics among odontocete species. Researchers compare the characteristics of pulses from different odontocete species based on studies in Japan and China.
- D 3. Verboom & Kastelein (Harderwijk Dolfinarium)-Structure of Harbour Porpoise, *Phocoena phocoena*, acoustic signals with high repetition rates. Measurements of the repetition rate, duration, and frequency characteristics of echolocation pulses were collected from stranded Harbour Porpoise in Holland. (Title change)
- D 4. Philips, Au, Nachtigall, Pawloski, & Roitblat (University of Hawaii)-Echolocation in the Risso's dolphin, *Grampus griseus*: a preliminary report. A captive Risso's dolphin trained for a basic echolocation task provides the first indications of echolocation in this species.
- D 5. Miller & Rasmussen (University of Odense)-The echolocation and social signals from white-beaked dolphin, *Lagenorhynchus albirostris*, recorded in Icelandic waters. Field recordings of pulses produced by echolocating white-beaked dolphins in Iceland provide the first data on this species.
- D 6. Fahner, Thomas (Western Illinois University), Ramirez, & Boehm (Shedd Aquarium)-Acoustic properties of Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, echolocation signals. Pulses from six, captive Pacific white-sided dolphins echolocating on three different targets provide details of this new species' biological sonar.
- D 7. Dubrovsky, and Giro. Modeling of the click production mechanism in the dolphin.

## **Section II: Auditory Systems in Echolocating Mammals**

The Auditory Periphery in Bats and Dolphins by Marianne Vater from the University of Potsdam, Manfred Kössl from the University of Munich and Darlene Ketten from Woods Hole Institute of Oceanography.

Bats and dolphins adapted and modified the basic mammalian mechanisms of peripheral auditory processing to the working frequency range of echolocation. The chapter reviews data on: (1) specializations of sound reception sites and sound conducting apparatus for underwater hearing in dolphins; (2) general adaptations of the cochlea of bats and dolphins for processing echolocation signals; and (3) evolution and design of exceptionally sharply tuned cochlear filter mechanisms.

### Current Research Papers on Bats-

1. Ketten (Woods Hole Institution of Oceanography)-Dolphin and Bat Sonar: Convergence, Divergence, or Parallelism.-The author provides a detailed comparison of the cochleae of many species of bats and dolphins and discusses the functional differences.
- D 2. Vater (University of Potsdam)-Cochlear anatomy related to bat echolocation. The paper describes cochlear adaptations for processing species-specific echolocation signals in CF-FM bats and FM bats.
- D 3. Kössl, Föllner & Faulstich (University of Munich)-Otacoustic emissions and cochlear mechanisms in echolocating bats. Authors investigate specialized cochlear filter mechanisms in bats with noninvasive measurements of otoacoustic emissions.



#### Current Research Papers on Dolphins-

1. Carder, Kamolnick, Schlundt, Elsberry, Smith, & Ridgway (Space and Naval Warfare Systems Center)-Temporary threshold shift in underwater hearing of dolphins.

Dolphin hearing sensitivity was tested before and after brief exposure to high amplitude sounds; results establish criteria for safe noise levels around marine mammals.

D 2. Schlundt, Carder, & Ridgway (Space and Naval Warfare Systems Center)-The effect of projector position on the hearing thresholds of dolphins (*Tursiops truncatus*) at 2, 8, and 12 kHz. Authors examined how dolphin hearing sensitivity is dependent on the location of the sound source and suggest that the low frequency portion of the cetacean audiogram might be re-evaluated based on projector position.

Central Auditory Processing of Temporal Information in Bats and Dolphins by Zoltan Fuzessery from University of Wyoming, Albert Feng from the University of Illinois, Ilya Glezer from City University of New York Medical School, and Alexander Supin from the Russian Academy of Science.

Analysis of rapidly changing temporal patterns of sounds by the central auditory pathway is crucial for biological sonar tasks and in the passive listening mode. This chapter reviews fundamental issues of temporal processing including temporal resolution, integration, specializations for processing of target distance information, neuronal responses to "natural" stimuli, and processing mechanisms in active and passive listening.

#### Current Research Papers on Bats-

D 1. Ellen Covey (University of Washington)-Midbrain integrative mechanisms and temporal pattern analysis in echolocating bats. This paper analyzes the functional role of excitatory and inhibitory ascending inputs to the auditory midbrain in shaping selectivity for temporal patterns of sound.

D 2. Fuzessary, and Lohuis (University of Wyoming)-Specializations for biosonar and passive hearing in a gleaning bat. The paper describes the functional organization of the pallid bat's auditory system focusing on features that serve the bats' need for specialization in both passive and active listening tasks.

D 3. Galazyuk, White, & Feng (University of Illinois)-Single neurons in the inferior colliculus of little brown bats display response hyper acuity to amplitude of sound pulses embedded in random-amplitude AM-pulse trains. This article focuses on temporal integration in the central auditory processing in FM bats.

D 4. Portfors & Wenstrup (Northeastern Ohio University)-Neural processing of target distance: transformation of combination-sensitive responses. This contribution discusses how neural response properties related to encoding target distance in the mustached bat change between the inferior colliculus, their probable site of construction, and the medial geniculate body.

D 5. Wenstrup, Leroy, Portfors, & Grose (Northeastern Ohio University)-Neural mechanisms underlying the analysis of target distance. This chapter describes mechanisms in the mustached bat that create neural responses selective for sonar target distance.

#### Current Research Papers on Dolphins-

D 1. Supin & Popov (Russian Academy of Science)-Temporal processing of rapidly following sounds in dolphins: evoked potential study. Using evoked potential methods on a live



dolphin, the authors measured the processing time for pulses in a train, thus providing good information on temporal processing in echolocation signals.

D 2. Glezer, Hof, Morgane, Friedman, Isakova, Josef, Nair, Parhar, Thengampall, Vengupal, & Yung (City University of New York School of Medicine)-Chemical neuroanatomy of cerebral auditory structures in brains of echolocating and non-echolocating mammals: The authors examine the hearing mechanisms of in the brains of mammals using morphochemical methods.

D Feature Extraction in the Auditory Cortex of Echolocating Bats by Nobuo Suga from the Washington University.

D Feature Extraction in the Mustached Bat Auditory Cortex by William O'Neill from the University of Rochester.

D The auditory cortex of the horse bat by William O'Neill from the University of Rochester.

D The auditory cortex of the little brown bat by Donald Wong from Indiana University.

D The auditory cortex of the big brown bat by Steven Dear from University of Chicago.

Cortical feature maps representing different aspects of information contained in biological sonar and communication signals are generated by divergent-convergent interactions of neurons. This chapter reviews data on cortical computational maps and the role of the corticofugal projections in self-organization of the central auditory system in bats. Such data are not available for dolphins because of restrictions in research methods for these species.

#### Current Research Papers on Bats-

D 1. Esser & Eiermann (University of Ulm)-Processing of frequency-modulated sounds in the *Carollia* auditory and frontal cortex. This chapter describes the processing of sound signals (predominantly FM) in the auditory and frontal cortex of the short-tailed fruit bat, *Carollia perspicillata*.

D 2. Jen, Sun, Chen, & Zhang (University of Missouri-Columbia)-Corticofugal regulation of bat midbrain auditory sensitivity. This report describes the short term corticofugal regulation of frequency tuning and spatial response area of the inferior collicular neurons in bats.

D 3. Kanwal, Peng, & Esser (Georgetown Medical Center)- Convergent and separate processing of communication and echolocation sounds in the bat cortex. This report compares the basic neural response patterns in different cortical areas to echolocation and communication sounds and discusses convergent and separate processing of echolocation and communication information within single cortical neurons.

D 4. Radtke-Schuller (University of Munich)-The auditory cortex of the horseshoe bat: neuroarchitecture and thalamic connections of physiologically characterized fields. Combined neurophysiological and neuroanatomical techniques were used to map the functional subdivisions of the auditory cortex.

D 5. Suga, Zhan, Olsen, & Yan (Washington University)-Modulation of frequency tuning of thalamic and midbrain neurons and cochlear hair cells by the descending auditory system in the mustached bat. Auditory cortical neurons mediate a highly focused positive



feedback, incorporated in widespread lateral inhibition via corticofugal projections to subcortical centers of the bat brain.

D 6. Wong & Chen (Indiana University School of Medicine)-Relationship between frequency tuning and delay tuning in the FM bat, *Myotis lucifugus*. (this was requested as addition after approval by publisher, try to add, Wong's only first author paper), added since submitted to publisher.

### **Section III: Performance and Cognition in Echolocating Mammals**

A Comparison of Performance and Cognitive Abilities in Echolocating Bats and Dolphins by Heidi Harley (University of Florida) & Mitch Masters, Ohio State University.

In this chapter, the authors discuss what is known about the echolocation abilities of bats versus dolphins and species differences. Authors describe results of passive listening studies and basic detection and discrimination abilities. The dynamic nature of signals and how they change during target detection and orientation is examined. Authors report how echolocation changes for a stationary versus a moving detection task. The impacts of background noise and clutter on echolocation abilities in bats and dolphins is addressed. Information from both field and laboratory studies is included. Future areas of study include the role of learning in echolocation, aspect dependency in target identification, and imagery or representation of echolocation signals.

#### Current Research Papers on Bats-

D 1. Miller & Futtrup (University of Odense)-How extrinsic sounds interfere with bat biosonar. The directional properties of hearing and signal production, together with restricted temporal auditory windows, help to protect bat sonar from interference. (author change since publisher reviewed)

D 2. Uwe Schmidt, Miriam Schlangen, Philipp Krasemann, & Patrick Höller (University of Bonn)-The significance of multimodal orientation in phyllostomid bats. Studies on the contribution of visual, echoacoustic, and intrinsic spatial information to the orientation behaviour in *Desmodus rotundus* and *Phyllostomus discolor*.

D 3. Von Stebut & S. Schmidt (University of Munich)-Frequency processing at search call frequencies in *Eptesicus fuscus*: adaptation for long distance target detection? The big brown bat is able to perceive modulation frequencies as produced by wingbeating insects, similar to bats emitting short CF/FM signals and therefore may use this information for long distance target detection.

4. Sabine Schmidt (University of Munich)-Auditory categories in bat sonar: How to make use of complex spectra. This paper addresses the perceptual dimensions available to the bat, *Megaderma lyra*, for the classification of echo spectra.

D 5. Siewert, Schillinger, & S. Schmidt (University of Munich)-Forward masking and its consequences for echo perception in the gleaner bat, *Megaderma lyra*. By studying forward masking abilities in bats, the authors examine how echolocating bats process weak echoes shortly after emitting strong outgoing pulses.

D 6. Surlykke (University of Odense)-Detection thresholds depend on the number of echoes in the big brown bat, *Eptesicus fuscus*. Distance detection thresholds were measured



using a computer DSP-based system and custom software to examine the effects of the number of echoes.

D 7. Masters & Raver (Oregon State University)-Bats can learn to use echoes having unfamiliar time-frequency structures. Author describes the abilities of bats to learn and use new echolocation-like signals.

#### Current Research Papers on Dolphins-

1. Nachtigall (University of Hawaii)-Target discrimination in bottom sediments in dolphins. Authors document the ability of a dolphin to discriminate targets buried on the ocean bottom.

D 2. Zaslavsky (Tel Aviv University)-Time and frequency analysis in the dolphin. The author describes the frequency and time domain analysis of tone-like signals and short pulses in the dolphin's auditory system.

D 3. Harley (University of Florida)-Identity versus conditional cross-modal matching in the bottlenose dolphin. The author conducted experiments on captive dolphins to examine the world as dolphin perceive it using echolocation.

4. Roitblat (University of Hawaii)-Recognition Processes in Echolocation. Object recognition in dolphins depends on more than purely sensory-driven processes, including higher cognitive mechanisms such as memory, judgment, and inference.

#### **Section IV: Ecological and Evolutionary Aspects of Echolocating Mammals**

D How Evolution Perfected Bat Echolocation for their Unique Ecology-by Elizabeth Kalko from the University of Tübingen, Annette Denzinger from the University of Tübingen, and Gareth Jones from the University of Bristol.

Scientists studying bats have advanced beyond basic species characteristics and field studies to examine signal design in the context of ecological factors. The authors discuss recent findings on the coevolution of insect prey and bat predators.

#### Current Research Papers on Bats-

D 1. Schnitzler, Kalko, & Denzinger (University of Tübingen)-The evolution of echolocation and foraging behavior in bats. Authors discuss the role of echolocation for the characterization of small single targets (prey) and large extended targets (vegetation and background) in the context of hypotheses on the evolution of echolocation.

D 2. Houston, Boonman, & Jones (University of Bristol)-Do echolocation signal parameters restrict bats' choice of prey?-The paper shows that prey size distribution is related to echolocation signal wavelength and duration, and target strength.

D 3. Fenton (York University)-Aerial-feeding Bats: Getting the Most out of Echolocation. This contribution examines the various situations in which bats use echolocation, considering the implications for signal design, including aspects of frequency, timing, and signal strength.

D 4. Houston and Jones (University of Bristol)-Discrimination of prey during trawling in the insectivorous bat, *Myotis daubentonii*. Two-alternative choice experiments were used to address the question of whether echolocating bats actively select certain types of prey.

D 5. Jones & Barlow (University of Bristol)-Cryptic species of echolocating bats. The ecology and evolution of bat species that look the same to use, but differ in their echolocation calls.

D 6. Speakman, Lancaster, Ward, Jones, & Cole (University of Aberdeen)-The energy cost of stationary echolocation in small insectivorous bats. This paper discusses new measurements of the energy costs of echolocation in perched bats which have implications for our



understanding of the evolution of echolocation in bats.

D 7. Rydell (University of Sweden)-Evolution of bat defense in moths (Lepidoptera): alternatives and complements to ultrasonic hearing. The paper describes behavioral strategies employed by deaf, potential prey, insects to avoid bat predation.

D 8. Tougaard, Miller, & Simmons (University of Odense)-The role of arctiid moth clicks in defense against echolocating bats: interference with temporal processing. A review of the current theories of the function of moth clicks as a defense mechanism against echolocating bats.

D 9. Faure & Hoy (Cornell University) -Auditory adaptations in katydids for the detection and evasion of bats. This paper uses a neuroethological approach to examine the physiological responses of a prominent central auditory interneuron-the large fibre-in a nocturnal katydid (bushcricket), as an evolutionary adaptations for the detection and evasion of predatory, insectivorous bats.

D Functional Aspects of Echolocation in Dolphins by Denise Herzing from the Wild Dolphin Project and Manuel dos Santos from the Institute Superior de Psicologia.

In this section, authors concentrate on dolphin echolocation in relationship to the ecology of the species. Only recently, has a diversity of odontocete species been examined for echolocation abilities. Field studies on dolphin echolocation and ecology are relatively new.

#### Current Research Papers on Dolphins-

D 1. dos & Almada (Institute Superior de Psicologia)-A case for passive sonar: analysis of click train emissions by bottlenose dolphins in a turbid estuary. Authors show through quantitative analysis that in some ecological contexts where abundant echolocation emissions would be expected during feeding, sonar production by wild dolphins actually is low, suggesting that other sensory modes are preferentially used when the "mixed blessings" of echolocation become costly.

D 2. Herzing (Wild Dolphin Project)-Social and non-social uses of echolocation in Atlantic spotted dolphins, *Stenella frontalis*, and bottlenose dolphins, *Tursiops truncatus*. The author describes species and social context differences in echolocation of wild dolphins.

D 3. Watkins and Daher (Woods Hole Institution of Oceanography)-Variable spectra and non-directional character of clicks from near-surface sperm whales (*Physeter catodon*). The paper describes the variability in frequency and level of clicks typical of sperm whales near the surface and the non-directional character of these sounds which propagate well whether the head is submerged or raised well out of the water.

4. Blackwood, Evans, Elsberry & Stiessen (Texas A & M University)-Dolphin echolocation during foraging: the role of habitat. Authors examine characteristics of echolocation pulses produced by wild dolphins and how they change with habitat type.

D 5. Lammers, Au, & Aubauer (University of Hawaii)-A comparative analysis of pulsed emissions of a free-ranging Hawaiian spinner dolphin (*Stenella longirostris*). The study documents characteristic differences and similarities between burst-pulse signals, believed to play a social function, and echolocation click trains.

D 6. Lucke and Goodson (Loughborough University of Technology)-Fishing in the dark-an acoustic analysis of wild dolphin echolocation behaviour. The authors describe the characteristics of echolocation signals from a wild dolphin while this animal is foraging.

D 7. Moreno, Kamminga, & Cohen (Technical University of Delft)-Patterns of



pulse repetition frequency of Amazon River dolphins, *Inia geoffrensis*, during sexual behavior in captivity. The authors describe sounds produced by the endangered Amazonian River Dolphin.

D 8. Blomqvist & Amundin (University of Goteborg and Kolmarden Zoo)-High frequency, burst pulse sounds in intra-specific communication in the bottlenose dolphins, *Tursiops truncatus*. The authors examine whether echolocation pulses also can be used in agonistic encounters by dolphins. (Title change since approved by publisher)

## **Section V: Echolocation Theory, Analysis Techniques, and Applications**

Recent Trends in Echolocation Signal Analysis and The Real World Applications by David Helweg, and Patrick Moore from Space and Naval Warfare Systems Center, and James Simmons from Brown University.

In this chapter, authors discuss differences in sound propagation and reverberation in air and the aquatic environment. Authors present current models for echo detection, recognition, discrimination, and imaging. Several new software systems used for echolocation signal analysis will be summarized. How acoustically-guided robots (based on bat models) use echolocation will be described. Future directions of research, analysis, and applications will be listed.

### Current Research Papers-

D 1. Palakal, Wong, & Chen (Indiana University School of Medicine)-A Biologically Plausible Framework Leading to Auditory Perception in FM Bats. The paper addresses cortical mechanisms of auditory scene analysis in the FM bat, *Myotis lucifugus*.

D 2. Parsons (University of Bristol) & Obrist (Swiss Federal Institute for Forest, Snow & Landscape Research)-Recent methodological advances in the recording and analysis of chiropteran biosonar signals in the field. The authors discuss how improvements in techniques for the recording and analysis have allowed field biologists to use biosonar for ecological studies of bats.

D 3. Obrist, Boesch, Flükiger (Swiss Federal Institute for Forest, Snow & Landscape Research) and Dieckmann (Fraunhofer Institute for Integrated Circuits, Erlangen)-Who's calling?-Acoustic bat species identification revised with synergetics. The author describes a technique for quick and economic recording, classification and identification of echolocation signals suitable for monitoring biodiversity of echolocating bats.

D 4. Kuc (Yale University)-Biomimetic sonar recognizes objects from echoes. Using a human-made sonar with a moveable center transducer, flanked by two rotating receivers (ears), the author examines useful features in echoes for object recognition.

5. Goodson (Loughborough University of Technology), Amundin (University of Stockholm), Lockyer (Cambridge), & Larsen-Aversive sounds and the harbour porpoise-devising a more effective acoustic deterrents for fishing nets. Investigations into what constitutes an 'aversive' sound for the harbour porpoise and the implementation and testing of a, new-technology based, programmable acoustic deterrent to reduce small cetacean by catch in commercial gillnets.

D 6. Gannon, W. L., O'Farrell, M. J., Corben, C. And E. J. Bedrick (University of New Mexico)-Analysis and interpretation of field recorded bat echolocation calls using analog.-Authors summarize the use of software and AnabatII detector for taxonomic classification of



different species of bats in the field.

D 7. Walker, Peremans, & Hallam-An investigation of active reception mechanisms for echolocators. A robotic sonar head is employed to investigate how an echolocator with mobile pinnae can estimate the 3D position of a target based on analysis of a series of interaural intensity differences. (title and author change since publisher has seen).

D 8. Aubauer, Au, Pawloski & Nachtigall (University of Hawaii)-Classification of realistic phantom targets in a dolphin echolocation experiment. Description and first experimental results of a new method of acoustically simulating real underwater targets to a dolphin in an echolocation experiment.

D 9. Altes (Chirp Corporation)-Models for parameter estimation in animal echolocation. Parameter estimation in using top-down and bottom-up processing, its application to a revised SCAT model and to high resolution SAS imaging, and its relationship to RAKE and matched field processing in human-made systems.

D 10. Goodson, Flint (Loughborough University) and Ted Cranford (San Diego State University)-The harbour porpoise (*Phocoena phocoena*)-modeling the sonar transmission mechanism. Computer modeling methods, based on dissection and X-ray CAT scan data, are used to dynamically investigate sonar pulse propagation through the melon and associated structures of the head of the harbour porpoise.

D 11. Andre (University of Las Palmas de Gran Canaria) and Kamminga (Delft University). Harmonic fluctuations in echolocation click train patterns of odontocetes, an intrinsic event series analysis.

12. Kamminga & Stuart (Delft University of Technology)-A model forming of odontocete sonar signals. Authors apply the Gabor wavelet analysis to individual clicks and click trains of 18 species of odontocetes.

D 13. Schotten, Au, Lammers, & Aubauer (University of Hawaii). Echolocation recording and localization of spinner dolphins (*Stenella longirostris*) and pantropical dolphins (*Stenella attenuata*) using a four hydrophone array. Characteristics of pulses and foraging behavior are described for a population of wild dolphins.

## **Section VI: Possible Echolocation Abilities in Other Mammals**

D Pinnipeds and the Echolocation Issue in the Year 2000 by Ronald Schusterman, David Kastak, and Levenson from the University of California, Hayward.

In this section, the authors examine the history of study of possible echolocation abilities in pinnipeds. Authors emphasize future directions of research that might provide evidence to support or refute the echolocation theory in this group of mammals.

### Current Research Papers on Pinniped Echolocation-

D 1. Awbrey (Hubbs-Sea World Research Institute), Thomas (Western Illinois University) & Evans (Texas A & M University)-Ultrasonic sound production in a captive leopard seal, *Hydrurga leptonyx*. A captive study on a leopard seal eating live fish documented ultrasonic pulses that are suggestive of echolocation.

D 2. Evans (Texas A & M University), Thomas (Western Illinois University), & Davis (Texas A & M University)-Sounds used during underwater navigation by a Weddell seal, *Leptonychotes weddellii*, carrying a video camera. Pulse trains were produced



by a Weddell seal wearing a video camera as it approached a breathing hole from under water and investigated fish.

D Review of Echolocation Studies in Insectivores and Rodents-by Jeanette Thomas and Mersedeh Jalili from Western Illinois University.

This paper reviews research conducted on shrews and rodent echolocation through the 1980s and suggests that with technological advances the topic should be studied further. New data will be provided on orientation studies in the least shrew and analysis of pulse characteristics for the least shrew, short-tailed shrew, and Norway rat.

Review of Echolocation Studies in Baleen Whales by Chris Clark from Cornell University.

The author reviews evidence for echolocation in baleen whales and provides some new data that is suggestive of such an ability.

### **Glossary**

An alphabetized list of terms with simple definitions will appear at the end of the book.

### **Publications, Abstracts, and Presentations Related to Project**

Echolocation in Bats and Dolphins, J. A. Thomas, M. Moss, and M. Vater, eds.  
Anticipated publication 2000. The University of Chicago Press, 600 pp.